THE POLYCHAETE CERATONEREIS TRIDENTATA AS A PEST OF THE SCALLOP AEQUIPECTEN GIBBUS

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Because of the importance of clams, scallops, mussels, and oysters as a source of food, the biology of bivalve mollusks has received much attention. Much ecological research has centered on the associates of these bivalves, in recognition of the possibility that they may destroy the bivalves, or restrict their growth or reproduction, and, in this manner, may compete with man's fullest utilization of the bivalve populations. These potentially detrimental associates include predators that feed on the mollusk, fouling organisms that attach to the shell, commensals and ectoparasites that live between the shells, invaders that live in the shell itself, and endoparasites that live within the tissues and organs of the bivalve.

The diverse organisms that can be termed "invaders" of the shell usually receive little consideration until, under optimal environmental conditions, a population "bloom" of the invader damages the shells sufficiently to cause mortalities or interfere with the processing or marketing of the shellfish. Outstanding examples of organisms that invade the shells of oysters are boring sponges (*Cliona* species), spionid polychaetes (*Polydora* species), and a fungus (Korringa, 1952). Usually the relation of such species to their host is quite distinct from that of the commensal or parasitic organisms, such as pinnotherid crabs, that live between the bivalve's shells. The species that invade the shell often have a detrimental effect upon their host, and to this extent, may consequently be considered parasites.

Since 1958, the calico scallop has been the object of a small commercial fishery on the North Carolina coast; however, the biology of this species has received little attention. Inasmuch as they can affect the population dynamics of the scallop, the enemies of this species, including its parasites, are important to this fishery.

The spionid polychaete, *Polydora websteri* Hartman, has long been considered a pest of bivalves. It penetrates the calcareous shells of oysters, scallops, and mussels, where its presence may stimulate the mollusk to secrete extra layers of shell around the worm's burrow. In this manner, *Polydora* causes its host to divert energy to shell deposition, detracting from its host's condition and suitability for market, and perhaps leaving its weakened host prey to other enemies and diseases (Lunz, 1940; Mackin and Cautheron, 1952; Medcof, 1946; Owen, 1957; and others). The typical deposits of shell around *Polydora websteri* are termed "mud blisters" because of their characteristic dark color and mud inclusions.

In January, 1959, large brown blisters were found in the upper valves of two calico scallops (*Aequipecten gibbus*), of a group of 20 which had been dredged off Ocracoke Island, North Carolina. The observed blisters contrasted with mud blisters produced in this bivalve in response to *Polydora websteri*, which is common in this area (Hartman, 1945). Whereas *Polydora* blisters were typically 5 to 15 mm. in greatest length in the scallops, these blisters were larger, 20 and 25 mm. in length. The interior of one blister communicated with the mantle cavity of the scallop through a hole in the scallop's mantle. Both blisters harbored an annelid identified as *Ceratonereis tridentata* (Webster, 1879) (Polychaeta: Nereidae), a species widely distributed along the Atlantic seaboard. Because such a relationship to mollusks had not been reported for this annelid species, a more extensive study was undertaken to determine the prevalence of such an infestation and its effects on scallops.

Dry Shells

Shell mounds outside a scallop shucking house at Salterpath, N. C., provided an easily accessible source of fresh shells for examination. These shells had been dredged commercially in March, 1961, off Core Bank, south of Ocracoke, N. C., near the source of the first infested scallops. Hundreds of shells bore blisters apparently caused by *Ceratonereis*. In an effort to obtain a quantitative sample,

Table I

Distribution of Ceratonereis blisters in Aequipecten gibbus

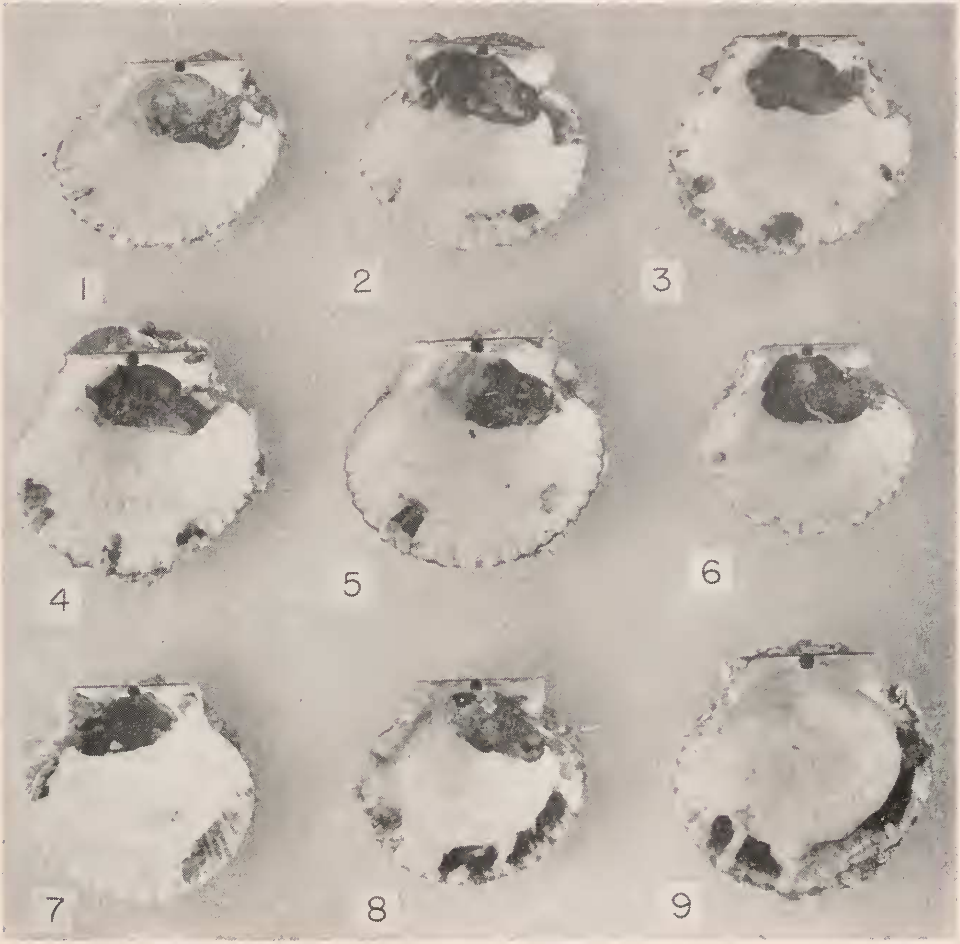
Position	Umbonal	Marginal	Totals
Upper valve	58	27	85
Lower valve	15	14	29
Totals	73	41	114

600 valves were examined for the presence of blisters. Only upper valves were used in order to avoid counting the same scallop twice. Recognition of *Ceratonereis* blisters was made difficult by an intense infestation of *Polydora* blisters. Because it was often difficult to distinguish between a marginal *Ceratonereis* blister and a series of contiguous *Polydora* blisters, those of questionable origin were not counted. *Ceratonereis* blisters were recognized in 81 of 600 shells examined (16%); *Polydora* blisters were noted for 116 of 300 shells (39%). The incidence of infestation approximated the level indicated by the earlier observations of *Ceratonereis* in *Aequipecten gibbus;* coincidentally, the *Polydora* infestation appeared to be much more intense.

Infection of Living Scallops

Fresh scallops dredged April 3, 1961, off Core Bank, were examined for the presence of blisters caused by *Ceratonereis tridentata*. As each specimen was opened, observations were made of possible damage to soft parts. Wherever there was any question as to the identity of the causative agent, every effort was made to locate and identify the inhabitant of the blister. *Ceratonereis* blisters were found in 118 of 486 scallops (24.3%). Of these, 10 (2%) contained double *Ceratonereis* infestations. Careful examination revealed that about 99% of the scallops were infested by *Polydora websteri* burrows and resulting blisters.

The discrepancy between these infestation levels and those obtained from dry shells may be attributed to possible destruction of blisters in the commercial shucking process and to the omission of infections in lower valves among the dry shells. *Ceratonereis* blisters occur in the lower (right) valve about one-third as often as



FIGURES 1–9. Interior views of *Aequipecten gibbus* shells showing blisters associated with *Ceratonereis tridentata*. Figures 1–8 show umbonal blisters; Figure 9 shows a marginal *Ceratonereis* blister. Figures 3–5, 8–9 also show smaller marginal blisters caused by *Polydora websteri*.

in the upper (left) valve (Table I), and when a corresponding correction is applied to the original level of incidence, there is satisfactory agreement.

NATURE OF BLISTERS

The interior of the valves of *Aequipecten gibbus* is typically composed of a smooth, pearly-white layer of calcium carbonate crossed by radiating shallow grooves that correspond to the radial ribs of the exterior sculpture. In many shells faint brown stains may be suffused through the shell layers adjacent to the dorsal wings (ears) and on the hinge line.

Blisters caused by *Ceratonereis* are composed of thin, dark brown layers of organic matrix (conchiolin) that contrast noticeably with the white interior of the shell (Figs. 1–9). They are not easily confused with the brownish suffusion near

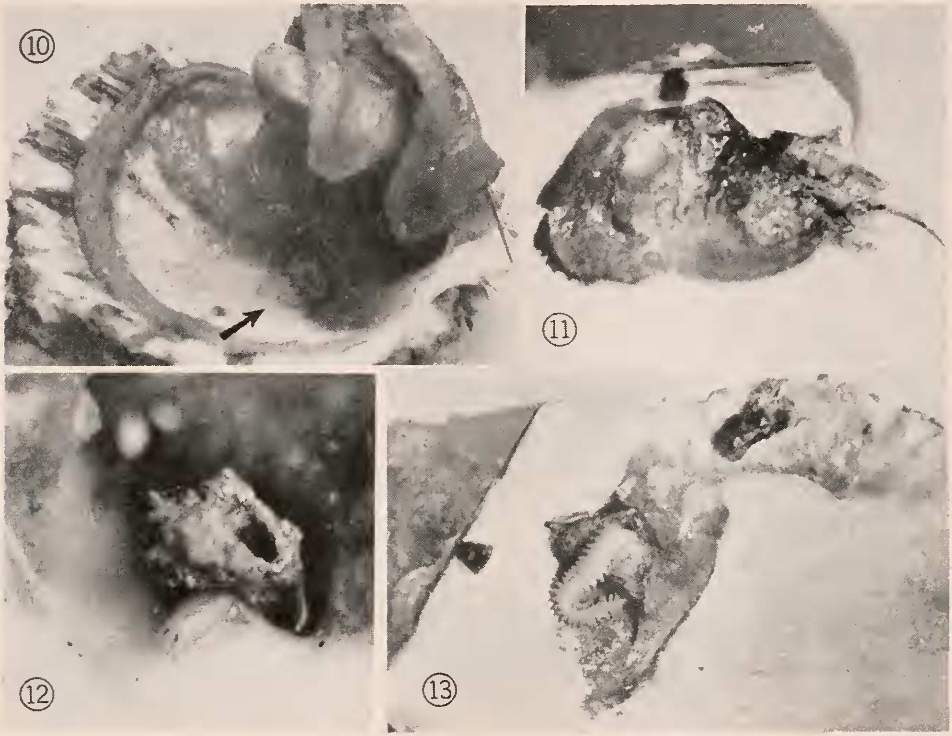


FIGURE 10. View into the mantle cavity of preserved scallop showing anterior end of *Ceratonereis tridentata* and mud tube projecting from mud-blister. Right valve removed and right mantle pulled aside.

FIGURE 11. Enlarged view of umbonal *Ceratonereis* blister showing natural perforation, and extension to anterior edge of shell.

FIGURE 12. Enlarged view of anterior end of *Ceratonereis tridentata* and mud tube projecting into mantle cavity through perforation in mantle and blister wall.

FIGURE 13. Umbonal blister with posterior end of *Ceratonereis tridentata* projecting from natural perforation. Exterior opening and blister development show clearly on anterior margin (to right).

the hinge nor with the red pigment of the exterior shell layers. Where the blister meets the margin, additional layers of conchiolin reinforce the edge. A similar thickening may be present around a perforation of the blister wall. At this stage, the conchiolin blister is still relatively flexible, although it becomes hard and brittle if dried. In later stages, white droplets of nacreous shell material are scattered over the dark foundation produced by successive conchiolin layers.

This nacreous material confers hardness to the blister wall, producing a thin crust around the invader, and as nacreous deposits accumulate, the dark color of the underlying blister becomes obscured. Where the nacreous crust has been broken, there are signs of repair involving both conchiolin and additional nacreous deposits. If the mantle has been prevented from returning to its normal position at the margin, a narrow rift may remain between the new and old layers of shell.

Generally, blisters caused by *Ceratonereis* are oval or crescent-shaped, depending on their position in the scallop shell. They may elevate the inner shell surface up to 4 mm., although most are only 2 or 3 mm. thick at the highest point. While the over-all surface area may vary considerably, from 1.3 to 8.5 $cm.^2$, most blisters occupy 3.5 to 4.0 $cm.^2$ of the interior surface. In other terms, the average blister occupies approximately 12% of the available surface of the affected shell. In extreme cases and where two infections occur in the same shell, up to 25% of its surface may be covered by *Ceratonereis* blisters. A more or less round perforation can be found on the central wall of many blisters (Fig. 11), its edges thickened as though extra layers of conchiolin have been deposited at this point.

TABLE II

Distribution of marginal openings in umbonal blisters

Position	Anterior opening	Anterior and posterior openings	Posterior opening
Upper valve	109	24	2
Lower valve	16	4	0
Total	125	28	2
%	81	18	1

This perforation is usually about 1 to 1.5 mm. in diameter. Adhering to the shell within a blister is a thin tube usually occupied by the polychaete. The tube is composed of fine sand grains loosely held together by mucus secreted by the worm. Usually, this tube is U-shaped, but in some cases, one end extends through the perforation beyond the edge of the blister (Figs. 10, 12). Where a functional opening to the exterior occurs at the shell margin, the channel may be as small as 0.3 mm. in diameter or as large as 2.5 by 1.5 mm. in cross-section. It is often somewhat hidden between subsequent deposits and the old shell layer. Usually, however, there is no external manifestation on the scallop shell of its internal deformation by *Ceratonereis*.

A series of *Ceratonereis* blisters in the calico scallop are shown in Figures 1–9. These blisters fall into two principal types on the basis of their shape and position in the scallop shell. The more abundant type (Figs. 1–8) is umbonal in position, *i.e.*, located under the umbo, dorsal to the adductor muscle or "heart" of the scallop; the other (Fig. 9) is marginal in position, located outside the pallial line (where the retractor muscles of the mantle attach to the shell). Marginal blisters are generally narrow and arched or crescentic, following the curvature of the margin, while umbonal blisters are more or less oval, usually with one or more extensions to the margin near the wings. Approximately 65% of the blisters caused by *Ceratonereis* occur in the umbonal position (Table I). As noted above, about 75% occur in the left valve, which is the upper valve in the normal orientation of the scallop. Most umbonal blisters have an arm that extends to the anterior margin immediately adjacent to the byssal notch, where the anterior wing joins the anterior shell border (Fig. 13). About 20% of umbonal blisters also possess a posterior extension across the posterior wing (Table II). Presumably both served at one time as a passageway for the annelid, but such channels to the exterior may have been closed by subsequent shell deposits. Independently of any marginal outlet, many blisters communicate with the scallop's mantle cavity through a perforation of the mantle and the conchiolin layer (Figs. 10–13).

Annelid Agent

Specimens of the annelid *Ceratonereis tridentata* were found in most blisters, sometimes with the anterior parts projecting into the mantle cavity from a hole in the blister (Fig. 12). Occasionally, when the host scallop had died before it was opened for examination, the blister was empty and a *Ceratonereis* was sometimes found crawling about on the exterior of the shell. Specimens of *C. tridentata* also were found frequently among the epifauna of the scallop shells, without apparent relation to the presence or absence of internal blisters. Several other species of nereid polychaetes may occur in this epifauna, from which this invasive species should be distinguished.

Ceratonereis tridentata has been adequately described by Hartman (1945, 1951), who has reported it as occurring in shelly bottoms from New Jersey to Texas. Specimens of *C. tridentata* recovered from blisters in the calico scallop measured 20 to 50 mm. in length and 1 to 2.5 mm. in width.

Effect on Scallop

Without doubt, the observed *Ceratonereis*-associated blisters were formed by the scallop's mantle in response to its irritation by this annelid. In addition to its deformation of the shell, this annelid clearly affects the soft parts of the host scallop. To a minor degree, the natural symmetry of the scallop tissues may have been distorted by the volume of the *Ceratonereis* blister, but a greater distortion may occur as a result of direct contact of the annelid with the tissues. The blister cavity typically communicates with the scallop mantle cavity through a perforation of the mantle. In the more abundant umbonal blisters, this mantle perforation occurs a short distance anterior and dorsal to the adductor muscle. The edges of these perforations are smooth and thickened, rather than torn and ragged as would be expected if they had been the result of accidental damage or a single penetration by the annelid. More important, the gills were often reduced on the infected side when the opening to the blister lay close to the gill region. In an extreme case, only about one-fifth of the gill tissue remained on the affected side. This condition appears to be either the result of physical erosion of gill tissue by the movements of the annelid among the gills, or the result of actual ingestion of gill tissue by *Ceratonereis*. Since the activities of *Ceratonereis* have not been observed in living scallops, the cause of this damage cannot be fixed with certainty. A more obvious malformation of infested scallops was a marked reduction in the central visceral mass. The bright red and cream-colored gonads that usually comprise the greatest portion of the visceral mass were obviously atrophied in certain specimens. In extreme cases, the volume occupied by this mass was only 25 to 30% of its volume in normal, uninfested scallops of the same shell dimensions. These deleterious effects upon tissues were more frequently observed in scallops with umbonal blisters than in those with marginal blisters. Undoubtedly, the secretion of extra shell layers in response to irritation by *Ceratonereis* requires energy that might otherwise be utilized in the growth or reproduction of the scallop. Where the gills are damaged, the scallop's intake of food would also be impaired, with a consequent additional decline in the scallop's condition. The observed atrophy of gonads probably reflects the degree to which extra shell deposition and gill damage affect the scallop's over-all condition.

Mode of Infection

Unlike many bivalve mollusks, scallops cannot close their shells perfectly, so that a gap remains at both ends of the ligament. Water passes through these slits in the normal swimming activity of scallops (Gutsell, 1930). At the anterior end, this gap coincides with the byssal notch, a deep indentation of the margin that is more developed in the right valve. Very young scallops of other species (*Aequipecten irradians*, *Placopecten magellanicus*) attach to objects by byssal threads that pass through such an opening (Gutsell, 1930; Merrill, 1961). Presumably, young calico scallops also attach by a byssus through this notch. In this species, these narrow slits provide an unprotected natural channel for invasion by *Ceratonereis*. In the formation of an umbonal blister, *Ceratonereis* probably makes its entry through these openings, inserting itself between the mantle and the shell, and then constructs its U-shaped tube with both ends at or near the shell margin. It may perforate the mantle under the umbo, establishing an opening into the mantle cavity. First the conchiolin layer, then successive nacreous layers are deposited over the affected areas. Once the second opening is established, the scallop's deposition of shell material may close off the original entry without adversely affecting the annelid. Such a sequence seems a logical course for the formation of umbonal blisters, and fits the observed stages.

In the formation of marginal blisters, a similar sequence of events must occur, as a result of penetration by *Ceratonereis* between the mantle edge and shell in lateral and ventral regions. There, the attachment of mantle to shell along the pallial line apparently restricts the penetration of the annelid to a marginal zone and consequently delimits blister formation. As an additional possibility, *Ceratonereis* may be a secondary invader in marginal blisters initially caused by some other agent, although only two cases were recognized in which this sequence might have occurred. In shells of the sea scallop, *Placopecten magellanicus*, Merrill (1960) found marginal deformations which he attributed to mud and other foreign material introduced under the mantle edge. Various sessile organisms which occupied the resulting blisters were not considered to have initiated their formation. Judged by the success of *Ceratonereis* in penetrating between the shell and mantle in the dorsal regions, this annelid would be well adapted to exploit any physical injury to the ventral margin of the calico scallop. However, while *Ceratonereis* may be in some instances a secondary invader in marginal blisters.

there is no indication that *Ceratonereis* is ever a secondary invader in umbonal blisters.

Discussion

A number of agencies, both living and non-living, may cause withdrawal of a bivalve's mantle and the subsequent production of blisters around the site of irritation. As Merrill (1960) found in the sea scallop, non-living matter, accidentally introduced between the shells of a bivalve, may stimulate the secretion of a marginal blister, which isolates this material from the bivalve's soft parts. Merrill (1960) considered the introduction of mud and debris between the sea scallop's valves to be a result of nearby dredging operations. Considerable quantities of sand have been observed in freshly dredged calico scallops, in which the mantle edge had been forced away from the shell margin. If such a scallop were unable to clean itself, or if the mantle edge had been damaged, subsequent deposition of shell materials would produce a blister somewhat resembling the marginal blisters produced in *Placopecten magellanicus*. Some marginal blisters may be produced in *Aequipecten gibbus* by this mechanism, for scallops with damaged margins and several with a deposit of coarse sand enveloped by a conchiolin blister were observed, without trace of any biological agent responsible for the blister malformation.

The steps of blister formation are essentially the same in these cases of blisters caused by non-living materials as they are in biologically-caused blisters. In both cases, the initial reaction is the deposition of many thin conchiolin layers, followed by successive layers of white nacreous material. In time, the irregularity in the shell may be obscured by further nacreous deposits.

Probably the best-known animal that causes blister formation in bivalve mollusks is *Polydora websteri* Hartman, a well known pest of oysters which also occurs in many other bivalves, including the calico scallop. It can be distinguished with ease from *Ceratonereis tridentata*, for these two polychaetes belong in very different families. In contrast with *Ceratonereis tridentata, Polydora websteri* is usually slender and small, 20 mm. or less in length (Hartman, 1951). In calico scallops, *Polydora websteri* builds small, U-shaped tubes at the margin between the shell and mantle, where it accumulates mud and silt around its burrow (as in Figs. 3–5. 8). In time, layers of conchiolin wall off this accumulated material and the worm, and thus form a small, dark marginal blister, which averages about 7.5 by 9.0 mm. in these scallops. Some *Polydora* may tunnel obliquely through the shell, producing an often-twisted, U-shaped gallery up to 0.5 mm. in diameter. If such a gallery perforates the inner shell surface, the scallop may secrete resistant layers of conchiolin over the site of perforation. Many stages of *Polydora* infestation in *Aequipecten gibbus* have been recognized and observed, including some blisters formed over umbonal perforations, some of which had been covered and almost obliterated by subsequent nacreous deposits.

Interior blisters may be formed in reaction to several other living agents. Sponges of the family Clionidae characteristically inhabit calcareous materials, including the shells of living mollusks, often creating extensive systems of galleries and pores (Old, 1941; Hartman, 1958). Upon penetration to the inner shell surface of a living oyster, a boring sponge stimulates the secretion of extra shell layers, which form a yellowish or greenish blister over the penetration. In addition, pyramidellid gastropods of the genus *Odostomia* may cause marginal pockets similar to *Ceratonereis* blisters. By irritating the oyster's mantle in the course of feeding on the European oyster, *Odostomia eulimoides* causes the oyster to deposit shell layers around a small marginal pocket (Cole and Hancock, 1955). This ectoparasitic snail may then move into the resulting pocket, and feed upon the oyster's mantle from that position. In a similar fashion, the feeding of *O. scalaris* on the blue mussel may stimulate a similar deformation of the mussel shell.

These various blister-producing organisms derive different benefits from the association with their bivalve hosts. Like those on the outside of the shell, fouling organisms found within the shells of sea scallops primarily receive a secure attachment from their host. Additionally, they may receive a degree of physical protection from their predators. In a similar way, *Polydora* and boring sponges obtain protection from the shells they inhabit. In addition to protection from predators, the pyramidellid gastropods receive nourishment from their hosts, and may be considered as parasites. In view of its damage to the shell and its effects on the tissues of its host, *Ceratonereis tridentata* may be considered a parasite also. While it benefits from its association with a scallop, it may produce deleterious morphological and, probably, physiological changes in its host. However, because *Ceratonereis* commonly occurs in another habitat, living independently of the scallop, it should be considered as only a facultative parasite of the calico scallop.

No account of the food or feeding habits of *Ceratonereis tridentata* has been published. *Ceratonereis* specimens living in umbonal blisters with openings to the mantle cavity may receive some nourishment directly or indirectly from the scallop (*i.e.*, from the scallop's tissues or from its food). Although the erosion of the gills could be the result of their ingestion by *Ceratonereis*, it may be the result of physical erosion caused by the worm's presence in or passage through the gill region. The observed condition resembles the erosion produced in gills of the American oyster, *Crassostrea virginica*, by the presence of the oyster crab, *Pinnotheres ostreum*. The oyster crab ingests food filtered from the water by the oyster's gills, and in the process, its appendages damage the gills (Stauber, 1945). In a similar fashion, *Ceratonereis* may gather planktonic food from the scallop's gills, food which had been filtered and formed into mucous strands in transit to the scallop's mouth. Outside the scallop, a similar diet might be obtained from a plankton-feeder among the epifauna of the shell. Only laboratory observations of *Ceratonereis* could provide definitive information on its feeding habits.

Ceratonereis tridentata is indeed a pest of the calico scallop, with a 24% infestation, a relatively high level of incidence. It is interesting to compare the proportion of double infestations (2%) with the over-all level of infestation. By the law of probability, if the occurrence of a second infestation were independent of the presence in the scallop of a preceding *Ceratonereis* infestation, the incidence of double infestations would be about 5% (*i.e.*, the square of the incidence of single infestations). The observed incidence of double infestations is considerably lower than the theoretical level. Calico scallops being rather small, a typical *Ceratonereis* blister occupies a major part of the shell area (about 12%), and apparently may repel a second *Ceratonereis* infestation.

Because only the adductor muscle ("heart") of a scallop is utilized for food in this country, the presence of a *Ceratonereis* blister in its shells does not affect the preparation of a scallop for market. The principal effect of *Ceratonereis* is to reduce the growth and reproductive potential of the calico scallop. In this manner, *Ceratonereis* infestations may detract from the ability of the survivors of each fishing season to effect repopulation.

Undoubtedly, the superficial resemblance between *Ceratonereis* blisters and those caused by *Polydora* has delayed the recognition of *Ceratonereis* as a pest of scallops. Nevertheless, the incidence of *Ceratonereis* blisters has probably increased since 1958 in the local scallop population, as a result of the fishing operation itself. By introducing sand between valves and through injuries to mantle margins, the operation of dredging rigs probably leaves many of the surviving scallops more susceptible to *Ceratonereis* invasion. Concurrently, a similar increase has occurred since 1958 in the incidence of *Polydora* blisters in this scallop population.

Other evidence indicates that *Ceratonereis* may invade the shells of other scallops. Essentially similar blisters in the umbonal region have been found in shells of the bay scallop, *Aequipecten irradians*, and in one shell of the sea scallop, *Placopecten magellanicus*. In both cases, however, these were dry shells and no specimens of *Ceratonereis* were recovered. The incidence of such blisters and the identity of the causative agent should be investigated for these two species.

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Summary

The nereid polychaete *Ceratonereis tridentata* has been found occupying mud-blisters in the calico scallop, *Aequipecten gibbus,* from off North Carolina. Characteristic *Ceratonereis* blisters were found in 24% of live scallops examined. These blisters can be distinguished easily from those of *Polydora websteri* by their larger size and often by their location in the scallop shell. Blister cavities may communicate with the mantle cavity or with the exterior. Anomalous malformations of the gills and the gonadal mass often accompany blisters having communication with the scallop mantle cavity. *Ceratonereis tridentata* is a facultative parasite of this scallop, also occurring among the epifauna of its shell.

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